CLINAL VARIATION IN *Eucalyptus incrassata* LABILLARDIERE

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Abstract: Morphological variation of three closely related taxa of mallee eucalypts (*Eucalyptus incrassata, E. angulosa*, and *E. costata*) was examined. Morphological characteristics were quantified from samples collected over a range of environmental conditions in the Murray Mallee of southeastern Australia. Numerical analysis revealed that the three taxa form a continuous series; it is suggested that these taxa represent points in a cline of a single species. Revision of the nomenclature is proposed.

INTRODUCTION

Eucalyptus incrassata Labill., one of the most widespread mallee eucalypts, is found in mallee areas of Western Australia, South Australia, Victoria and New South Wales. Mallee communities, the most arid of the eucalypt-dominated communities of temperate Australia, are predominant between the 25 and 66 cm isohyets (Parsons 1966).

The natural distribution of *E. incrassata* is shown in Fig. 1. Disjunctions occurring on the Nullarbor and Roe Plains have been discussed by Parsons (1970).

The taxon *E. angulosa* Schauer represents a larger fruited form of *E. incrassata* with a more coastal distribution (Chippendale 1973). Its fruits tend to be more heavily ribbed than those of the smaller, smoother fruited *E. incrassata* (Burbidge 1947, Chippendale 1973) and it usually grows in white coastal sands in areas of 38-66 cm per year mean rainfall. *E. incrassata* occurs also in coastal areas but its range extends into the dryer areas of the Mallee where the average rainfall is 20-50 cm per year (Chippendale 1973).

The distinctions between *E. incrassata* and *E. angulosa* are not clear and identification of many specimens is difficult. As a result there have been many nomenclatural changes since the first description of the taxa in the nineteenth century.

The species *Eucalyptus incrassata* was described (1804) by Labillardière. He designated the type

Fig. 1 — Limits of *E. incrassata* distribution as shown by Parsons (1966), and sites of collections held by Australian Herbaria (Chippendale, unpublished data, 1977). □ *E. incrassata* Δ *E. incrassata angulosa*

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specimen from material he collected near Esperance Bay on the southwestern coast of Australia in December 1792 (Boomsma 1969). As with many other groups within the genus *Eucalyptus* many species described later were found to be synonymous with *E. incrassata*. Other forms, thought originally to belong to *E. incrassata* have been given the status of independent species.

The taxon *E. angulosa* is of particular interest as it has alternated frequently between independent species status and inclusion in *E. incrassata*. The taxon *E. costata* Behr. et Muell. ex Miquel is often used as an intermediate or linking form of *E. incrassata* and *E. angulosa*. A brief summary of the major changes of status of the taxa discussed is shown in Table 1.

The confusion regarding the status of the taxa *E. incrassata*, *E. angulosa* and *E. costata* appears to be due to the existence of a number of forms intermediate between each pair of taxa. Maiden (1922) gives examples of these forms, but their nature is unknown. Burbidge (1947) suggests that these taxa probably represent points along a graded series of variants.

The aim of this study was to find the nature of the forms intermediate between the taxa, and the relationships of the taxa themselves. The morphological characteristics of the major plant organs of trees covering a wide geographic range and encompassing the taxa *E. incrassata*, *E. costata* and *E. angulosa* were examined. Studies of geographic variation have proved useful in the revision of other groups of eucalypts: for example, Kirkpatrick (1974) used a geographic study of the 'blue-gum' group of eucalypts to revise the nomenclature.

To avoid confusion the name *E. incrassata* will be used here to include the taxa *E. incrassata* Labill., *E. costata* Behr, et Muell. ex Miquel and *E. angulosa* Schauer. When referring to the different forms of *E. incrassata* (i.e. typical form, *E. costata* form and *E. angulosa* form) the unattached epithets var. *incrassata*, var. *costata* and var. *angulosa* are used.

TABLE 1
A SUMMARY OF THE TAXONOMIC HISTORY OF *E. incrassata* AND CLOSELY RELATED TAXA.

Year	*Nomenclature*
1804	*E. incrassata* described by Labillardière, and validly named.
1843	*E. angulosa* described by Schauer, and validly named.
1855	*E. costata* described by Behr and Mueller (Mueller, 1855).
1859	*E. costata* validly named by Miquel.
1866	Bentham used the names *E. incrassata* Labill., *E. incrassata* var. *angulosa*; *E. costata* F. Muell. = *E. incrassata* var. *angulosa*.
1888	Mueller: *E. angulosa* Schauer and *E. costata* Behr et. Muell. both = *E. incrassata* Labill.
1934	Blakely uses the names *E. incrassata* Labill. *E. angulosa* Schauer and a new variety *E. angulosa* var. *ceratcorys*; *E. costata* Behr et. Muell. is listed a synonym of *E. angulosa* Schauer).
1947	Burbidge: *E. incrassata* Labill, *E. incrassata* var. *costata*, *E. incrassata* var. *angulosa* Bentham.
1969	Boomsma: *E. incrassata* var. *incrassata*, *E. incrassata* var. *angulosa* Benth; *E. costata* is included in *E. incrassata* although the variety is not specified.
1971	Brooker: *E. incrassata*, *E. angulosa* no mention of *E. costata*.
1971	Pryor and Johnson: Both *E. angulosa* and *E. costata* are local variants of *E. incrassata*.
1976	Chippendale: *E. angulosa* Schauer, *E. incrassata* Labill., *E. costata* F. Muell. = *E. incrassata* Labill.

MATERIALS AND METHODS

STUDY AREA

The study area comprised most of the south-eastern Australian Mallee as shown in Fig. 2. The climate of this region is semi-arid: average annual precipitation varies from 75 cm in the south to 25 cm in the northern extremities near Mildura. The rainfall is unreliable, with a variability (i.e. average deviation from mean annual rainfall as a percentage of the mean average rainfall) of around 30%. In terms of precipitation, evaporation and soil moisture storage there is a trend to increasing aridity moving east from the western extremities and north in the eastern section of the study area. Large areas of the mallee have been cleared for agricultural use and many of the collection sites used in our study were small relict roadside communities adjoining agricultural land.

SAMPLING METHODS

Trees were sampled at nine sites within the study area (Fig. 2). The number of trees sampled at each site ranged from seven to nineteen. The variation in sample size was due to the nature and size of the stands studied. It was considered an advantage to analyse all of the data gathered rather than to reduce the information by using standard population sizes. Pryor (1956) has suggested that the minimum population size for quantitative morphological studies on eucalypts is five trees. Trees were selected and sampled in a manner similar to that described by Green (1971). Voucher specimens of all samples used are held in the Monash University Botany Department Herbarium.

MORPHOLOGICAL CHARACTERISTICS

Measurements of adult leaf dimensions and capsule morphology were made for numerical analysis. The following measurements were made on ten randomly-selected capsules from each tree sampled: capsule diameter at half length (FW), diameter of

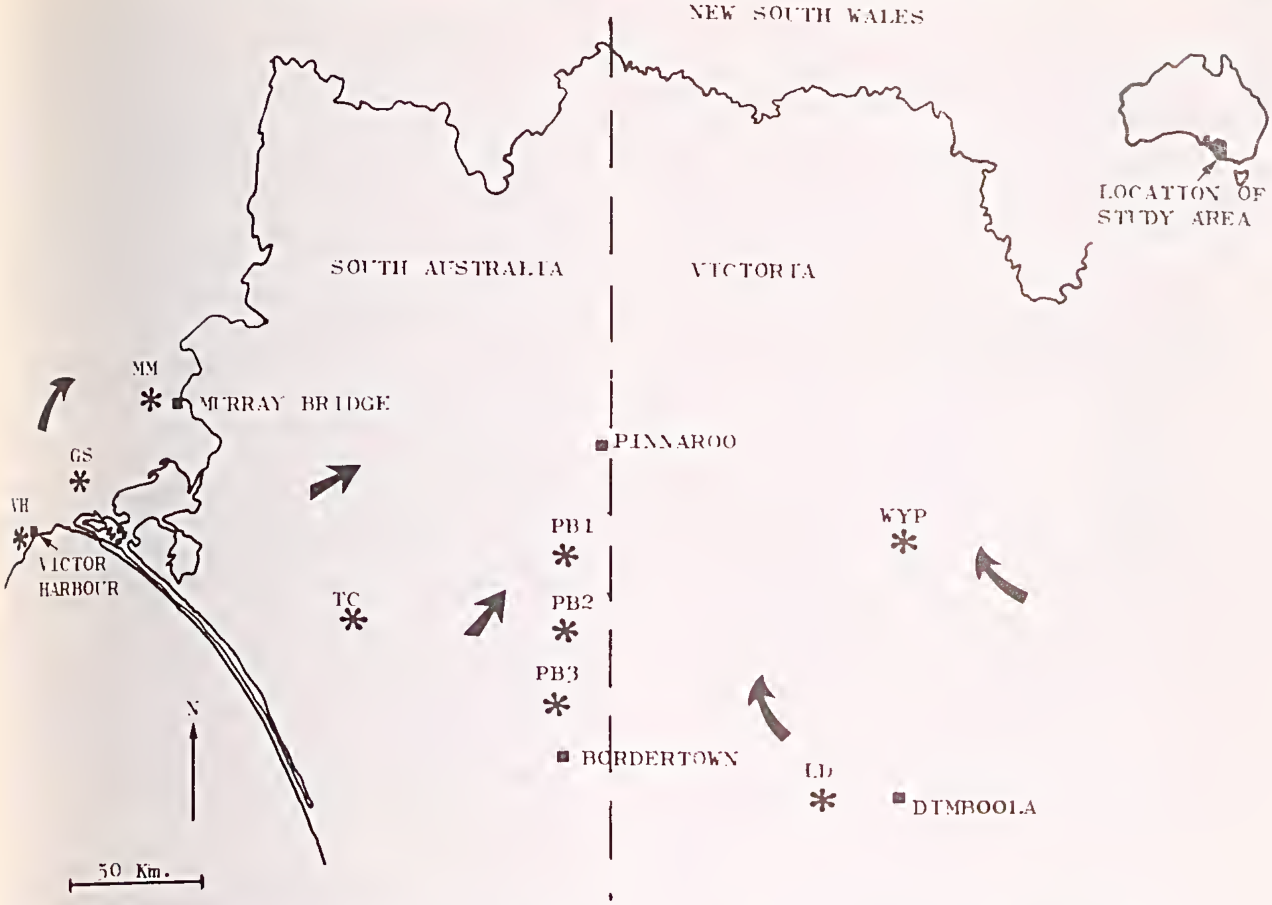

FIG. 2 — Map of the study area showing the location of collecting sites together with their codes e.g. MM. The large arrows indicate the gradient of increasing aridity moving inland. Exact locations of collecting sites are listed in Appendix I.

calycine ring (EW), capsule length (excluding pedicel) (FL), the number of valves per capsule (VN), the relative depth of valves (0 = valves exerted → 3 = valves deeply sunken) (VD), pedicel length (PC) and peduncle length (PD) (see Fig. 3). From these characteristics additional derived characters were calculated, these being the following ratios: FLW = FL/FW, W/E = FW/EW and C/D = PC/PD.

The degree of ribbing or angularity of the fruit surface has been quantified by assigning the following values to character FS (relative angularity of the fruit surface):

0 = 'smooth fruit': an absence of any longitudinal lines or ridges;
1 = 'striate fruit': longitudinal lines present; the lines are not raised significantly from the fruit surface;
2 = 'costate fruit': longitudinal ridges raised significantly above fruit surface, not as tall as broad, usually rounded summit;
3 = 'angular fruit': longitudinal ridges raised significantly above fruit surface, as tall or taller than broad, summit often sharp, triangular in section.

Burbidge (1947) used 'striate' to describe longitudinal ridges or lines which are apparent owing to shrinkage of non-sclerotised tissues; 'ribbed' was used when the ridges were deep enough to have been evident on fresh specimens. The implication is that some fruit capsules examined were collected whilst 'green' and have since suffered shrinkage during drying. The drying of fruit detached from the tree often results in a surface pattern not normally seen on fruit which have dried *in situ*. Wrinkling of the surface and more prominent striations are often the result.

In this study all characteristics of the fruit capsules were determined from mature fruits which had dried naturally on the tree. Wherever possible they were collected with the fruit valves open and seed still in the fruit. Old fruits tend to have surface features weathered away.

Morphology of the leaves was assessed by

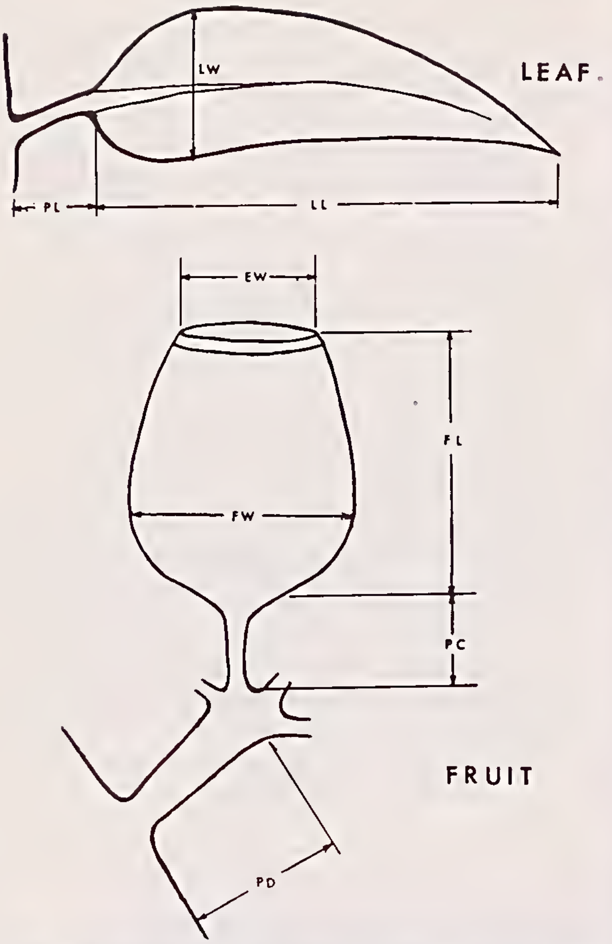

FIG. 3 — Illustration of the morphological characters of the leaves and fruit.

selecting the largest leaves of 10 branchlets from each tree, these leaves being regarded as representative of each tree (Larsen 1965). The following measurements were made on these leaves; leaf blade length (LL), leaf blade width (LW), petiole length (PL) (see Fig. 3). From these characters further ratios were derived; L/W = LL/LW, L/P = LL/PL.

ANALYSIS

The morphological data for the trees sampled was analysed using a Burroughs B6700 computer at Monash University and a PDP 10 at La Trobe University.

The following numerical methods were used to analyse the raw data:

i) *Factor Analysis* (Harman 1965), a method of data reduction. The variance of a set of variables is explained in terms of a set of fewer uncorrelated variables (factors). In most cases the number of factors accounting for the total variation is significantly fewer than the number of variables entered into the analysis. The program '*FACTOR*' with Varimax orthogonal rotation (Nie *et al.* 1970) was used in this study. This is an R-mode analysis which uses a correlation matrix.

ii) *Analysis of Variance and Student-Newman-Keuls Multiple Range Test* (*S.N.K.*) (Sokal & Rohlf 1969). Populations were checked for significant F-ratios, and significant differences between population means for each character were determined using the S.N.K. test. Analysis of variance and the S.N.K. test were performed on the data using a computer program described by Adams & Turner (1970).

iii) *Surface Trend Analysis* (Adams 1970). Population means for characters found to differ significantly between populations (using the S.N.K. test) were contoured using Surface Trend Analysis. The program CONTRS 4 (Adams 1970) was used to generate contour gradients for each character. The contours were then superimposed onto a map of the study area. The relationships between populations can then be assessed visually.

iv) *Differential Systematics* (Adams & Turner 1970). Differential systematics is a method which gives an indication of the total trend of several characters at once. Regions of rapid change are detected which indicate regions of differentiation within a taxon. The program DIFFSYS (Adams 1970) was used in this study.

v) *Hierarchical Grouping Analysis*. Hierarchical grouping analysis was used to cluster individual trees into groups whose members were more similar to one another than to any individual outside of the group (Lance & Williams 1967a). Many methods of producing a hierarchical classification are available (Lance & Williams 1967a, 1967b, 1968). The program HGROUP (Veldman 1967) was used in this study. This program employs a polythetic, agglomerative strategy based on within-group variance, in contrast to the commonly used similarity measures.

RESULTS

The morphological characters measured for *E. incrassata* show considerable variation. The means, standard deviations and ranges of values for the morphological characters are listed in Table 2. From this data and the scatter diagrams (Fig. 4) of selected pairs of variables, considerable variation within the taxon is apparent.

The morphological characters accounting for variation of *E. incrassata* were determined by Factor Analysis. The variation was accounted for by six factors. The percentage of the total variation accounted for by each factor and the characters correlated with each factor (ranked in order of correlation with the factor) are shown in Table 3. This indicates that the

TABLE 2
MORPHOLOGICAL CHARACTERISTICS OF *E. incrassata*

Code	*Character*	*Mean**	*Std. Dev.*	*Range**
LL	Leaf blade length	90.3	11.5	57.5 —127.1
LW	Leaf blade width	21.3	3.5	13.9 — 33.4
PL	Petiole length	17.0	2.7	12.0 — 24.0
L/W	LL/LW	4.3	0.7	2.3 — 6.26
L/P	LL/PL	5.4	0.9	3.87— 8.42
FL	Fruit length	13.5	2.4	7.7 — 22.1
FW	Diameter of fruit at ½ length	10.8	2.0	6.3 — 22.3
EW	Diameter of Calcine ring	9.2	1.6	6.38— 19.00
PD	Peduncle length	14.2	2.9	7.2 — 22.6
PC	Pedicel length	2.8	1.5	0.42— 8.07
FLW	FL/FW	1.3	0.15	0.98— 1.67
W/E	FW/EW	1.2	0.11	0.90— 1.50
C/D	PC/PD	0.19	0.09	0.00— 0.67
VN	Average no. of valves per fruit	3.1	0.2	3.0 — 4.0
VD	Relative depth of valves	2.3	1.8	1.0 — 3.0
FS	Relative angularity of fruit	2.1	0.8	0.0 — 3.0

*Where appropriate all dimensions are in mm.

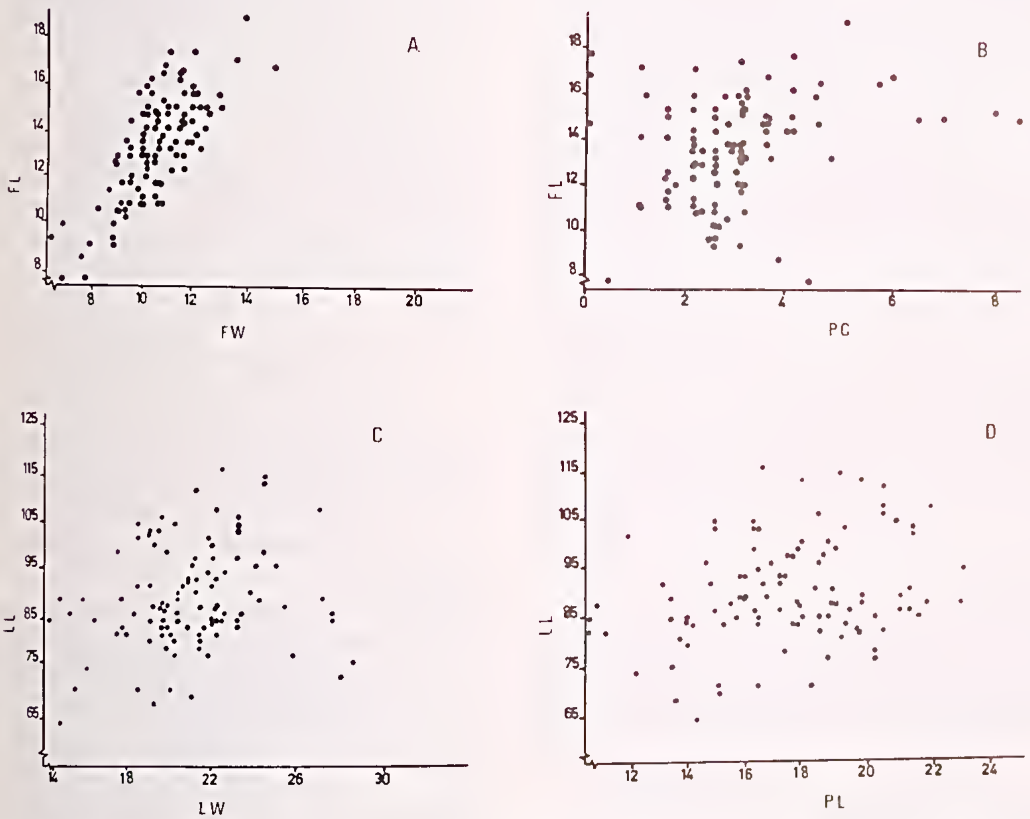

FIG. 4 — Scatter diagrams of several pairs of morphological characters. A. Fruit length (FL) v. Fruit Diameter (FW); B. Fruit length (FL) v. Pedicel length (PC); C. Leaf length (LL) v. Leaf width (LW); D. Leaf length (LL) v. Petiole length (PL). The scale of each axis indicates the length in millimetres.

first character listed for each factor is the best approximation to the factor.

The variation of *E. incrassata* can be accounted for by the characters FL, PC, LW, PL, LL, W/E (in descending order of percentage variation explained). The fruit dimension characters (FL, FW, EW) are highly correlated (all correlated to Factor 1, implying that the general shape of the fruit is similar over the range of fruit sizes. The 'angularity' of the fruit (FS) is also correlated to Factor 1, which implies a correlation between fruit size and 'angularity'. Examination of raw data and specimens collected shows that larger fruit are more angular than smaller fruit. The scatter diagram of FL versus FW (see Fig. 4) shows this correlation between the fruit length and diameter. There is a spread of values orthogonal to the main axis of the scatter, indicating some variability in the length-width ratio of the fruit. The character FLW is correlated to the second factor (Table 3); FLW, a measure of fruit shape, varies independently of the fruit dimensions. The character W/E is a measure of the degree of tapering of the upper half of the fruit. W/E is correlated to the sixth factor (Table 3), and is, therefore, independent of fruit size (FL, FW, EW) and basic fruit shape (FLW). The morphology of the fruit has three independent patterns of variation.

The character PC is correlated to both the uncorrelated characters PD and FLW. The narrow fruit (high values of FLW) tend to have long pedicels and where the pedicel is long there is also a trend towards long peduncles. The ratio between PC and PD (C/D) does not account for any more variation than the pedicel length itself and is highly correlated with PC (pedicel length).

The characters of the leaf vary independently from those of the fruit, with the exception of VN which co-varies with the width of the leaf blade. The three primary characters of the leaf (LL, LW, PL) account for different factors of the variation pattern. The scatter diagrams of combinations of these characters show that although a degree of correlation is evident there is a considerable spread of points orthogonal to the main axis. The lack of correlation between these two characters was expected as the samples collected showed a wide range of leaf shapes.

The total variation pattern of *E. incrassata* is composed of six independent factors. These are correlated to three independent characters of the fruit (FL, PC, W/E) and three independent characters of the leaves (LL, LW, PL). It is possible for any individual of *E. incrassata* within the study area, to possess a combination of any values in the range of these characters.

The nature of the variation (disjunct, clinal or random) can be assessed by analysis of the variation within and between populations of the taxa over a geographic range.

The morphological characters which have greater variations between populations than within populations were identified by Analysis of Variance and S.N.K. test (using the 0.01 level of significance) (Table 4).

The characters showing significant differences between populations are not the same as those accounting for the total variation pattern (from Factor Analysis). Some of the characters which account for the total variation have a higher variance within populations than between populations. The characters FS, FW, EW (Factor 1); LL (Factor 2); LW (Factor 3) do not show significant differences between the populations using the S.N.K. test.

The results from the S.N.K. test (Table 4) give an indication of a trend. Samples from the Victor Harbor (VH) and Goolwa-Strathalbyn (GS) populations appear to have significantly larger means for many characters than the samples from the Pinnaroo-Bordertown 2 (PB2) population.

TABLE 3
RESULTS OF *E. incrassata* FACTOR ANALYSIS

Factor	% of Variation Accounted for	Characters Significantly Correlated to Factor
1	30.6	FL, EW, FW, FS
2	21.9	PC, C/D, FLW
3	15.6	LW, L/W
4	12.5	PL, L/P
5	11.7	LL
6	7.6	W/E

TABLE 4
RESULTS OF THE S.N.K. TEST ON
E. incrassata POPULATIONS

The population codes are listed in order of decreasing magnitude of the population means for the character tested. The lines connect means which have no significant difference. Any two means connected by a single line are regarded as not being significantly different.

Character Tested	*S.N.K. Grouping of Populations*								
PL	MM	VH	LD	TC	GS	PB1	WYP	PB2	PB3
L/P	PB3	WYP	TC	GS	PB2	VH	LD	PB1	MM
FL	GS	VH	MM	PB3	LD	TC	PB1	PB2	WYP
PC	VH	GS	MM	LD	PB3	WYP	PB1	TC	PB2
FLW	GS	VH	MM	TC	WYP	PB3	PB2	PB1	LD
C/D	VH	GS	PB1	LD	MM	WYP	PB3	TC	PB2
VN	PB3	TC	VH	GS	MM	PB1	WYP	LD	PB2

The S.N.K. test provides information concerning characters which can be used for further analysis of the populations. Those characters which distinguish populations (and have a significant F value) were used for Surface Trend Analysis, Differential Systematics and Hierarchical Grouping Analysis.

The characters FL, PC, FLW, C/D (Figs. 5D, F, G, H) show definite, simple trends across the study area. Large values for the characters generally occur in the west and small ones in the east. The trends shown by these characters are of particular significance as the characters account for over half of the total variation of the individual samples (from Factor Analysis). The trends in the other characters are more complex. Some populations are quite distinct from those adjacent, causing distortion of the overall trends. The contour plot of FS (Fig. 5J) is an example of this type of map. The Tintinara-Culburra (TC) population (population d on Fig. 5J) is vastly different from any adjacent population. The west-east trend in FS is not obvious due to the influence of the contour lines surrounding population TC. Leaf width, LW (Fig. 5A) produces a complex pattern in which some local trends are detectable but in which there is no general trend across the study area.

The trends shown by the different contour maps were amalgamated using differential systematics. The rates of change between populations of all the character means are plotted as contours (Fig. 6). The number of contour lines between populations is an indication of the rate of change in the characters between the populations: the more lines the greater the change. Fig. 6 shows that there is a considerable rate of change between all populations. On the basis of character means the populations are distinct from one another, and the Surface Trend Analysis and S.N.K. results indicate that there are trends across the study area. Combining these results indicates that there may be a geographic sequence of populations covering the morphological range.

Referring again to the scatter diagrams (Fig. 4) there are no discontinuities in the points plotted. This implies that although the population means are distinct, the ranges of individuals in the populations overlap to such a degree that a continuous cluster of points is formed. This is shown clearly in Fig. 7. The range of fruit lengths overlap although the means are significantly different between populations.

Hierarchical Grouping Analysis was used to determine if, on the basis of a number of characters, the individual specimens would form distinct, interpretable groups. Two different character sets were analysed using HGROUP. These were the characters found to be significant in distinguishing populations using S.N.K., and the characters correlated to the factors produced by FACTOR.

The characters showing significant differences between populations (using S.N.K.), should be able to group the individuals into the original populations if the populations are well defined. The dendrogram resulting from using these characters in HGROUP is shown in Fig. 8. Six significant groups were formed, and of these, only two conform to any of the populations sampled. Group 1 (Fig. 8) is composed mainly of individuals from the Goolwa-Strathalbyn (GS) population, Group 3 is composed of individuals from Victor Harbor (VH). Individuals from these populations are not confined to these groups. Other individuals from these populations are found in some of the remaining groups. Group 2 accounts for most of the individuals from the Tintinara-Culburra (TC) and Monarto (MM) populations. Individuals from other populations are common in this heterogeneous group. The Wyperfeld (WYP) and Pinnaroo-Bordertown 2 (PB2) populations are found mainly in Groups 4, 5 and 6. These groups are heterogeneous in composition. The populations Little Desert (LD) and Pinnaroo-Bordertown 1 and 3 (PB1, PB3) are spread evenly throughout Groups 2, 4, 5 and 6.

The groupings in Fig. 8 show the lack of definition of the populations, some of which (GS and VH) do have unique distinguishing characteristics. Although the groupings show strong differences between eastern and western samples, samples from some populations are split between the two major groups. This result can be interpreted as repeating the findings of the previous analyses, i.e. that there is a trend across the study area. The results from Differential Systematics are also repeated. Using differential systematics the VH, GS and MM populations have the highest rate of change between them and they are well separated by Hierarchical Groupings Analysis.

The characters accounting for the factors produced by Factor Analysis were also used for HGROUP analysis. These characters were used to give an unbiased grouping of the individuals, the characters being uncorrelated. The groups of individuals produced by this analysis may represent a more natural grouping.

The population characteristics of the groups formed by this procedure are not as obvious as those from the S.N.K. characters. The western populations GS, VH and MM form a recognizable group (Group 6, Fig. 9) but this group includes several individuals from the east of the study area. The remaining groups (Groups 1-5, Fig 9) are heterogeneous.

The trends of groups and populations are not immediately obvious but it is possible to interpret the groupings from Fig. 9. They show that the populations from the western part are, in general, different from those in the eastern part, although considerable overlap

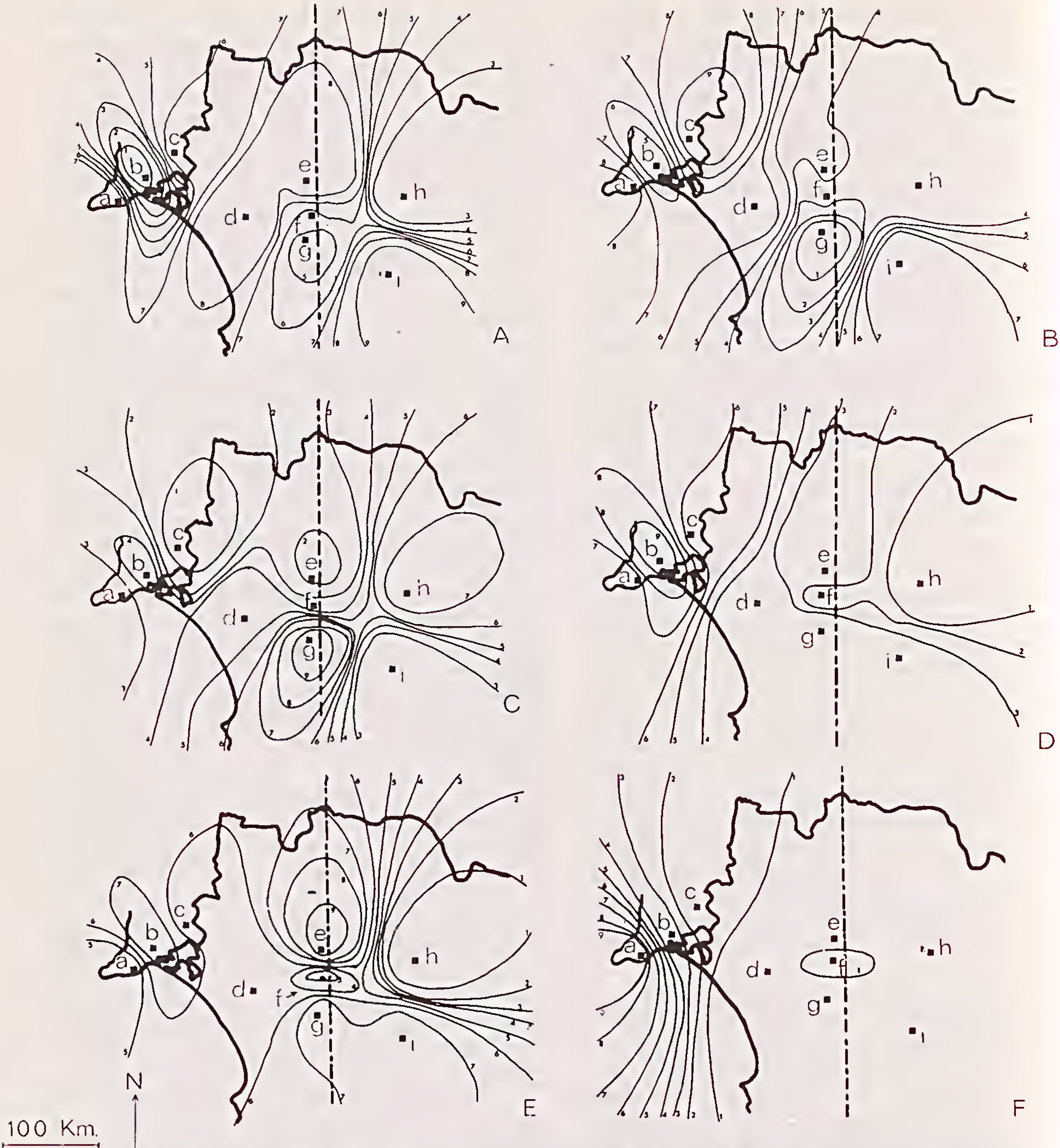

FIG. 5 — Contour plots of morphological characters of *E. incrassata*. The values of the contour lines represent ten divisions in the range of population means for each character. The smallest means have a contour value of less than one, the largest means a contour of greater than nine. A. Character LW; contour range 18.5-23.0. B. Character PL; contour range 14.0-19.0. C. Character L/P; contour range 4.8-6.3. D. Character FL; contour ıange 11.6-16.5. E. Character FW; contour range 9.4-11.8. F. Character PC; contour range 2.1-6.2. G. Character FLW; contour range 1.18-1.45. H. Character C/D; contour range 0.16-0.37. I. Character VN; contour range 3.04-3.28. J. Character FS; contour range 1.57-2.28. K. Character PD; contour range 13.3-17.80.
Population identity: a = VH, b = GS, c = MM, d = TC, e = PB1, f = PB2, g = PB3, h = WYP, i = LD.

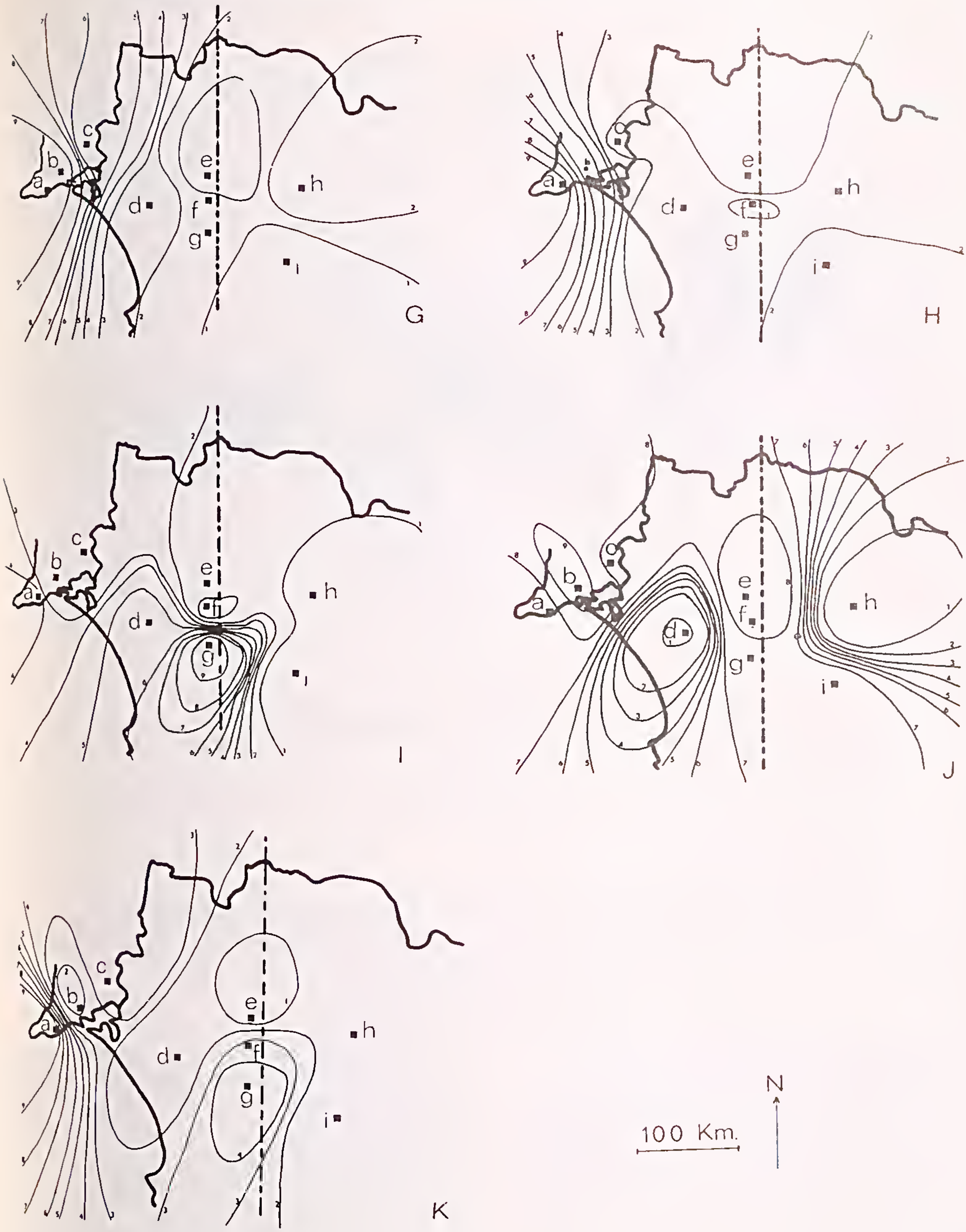

Fig. 5 (*continued*)

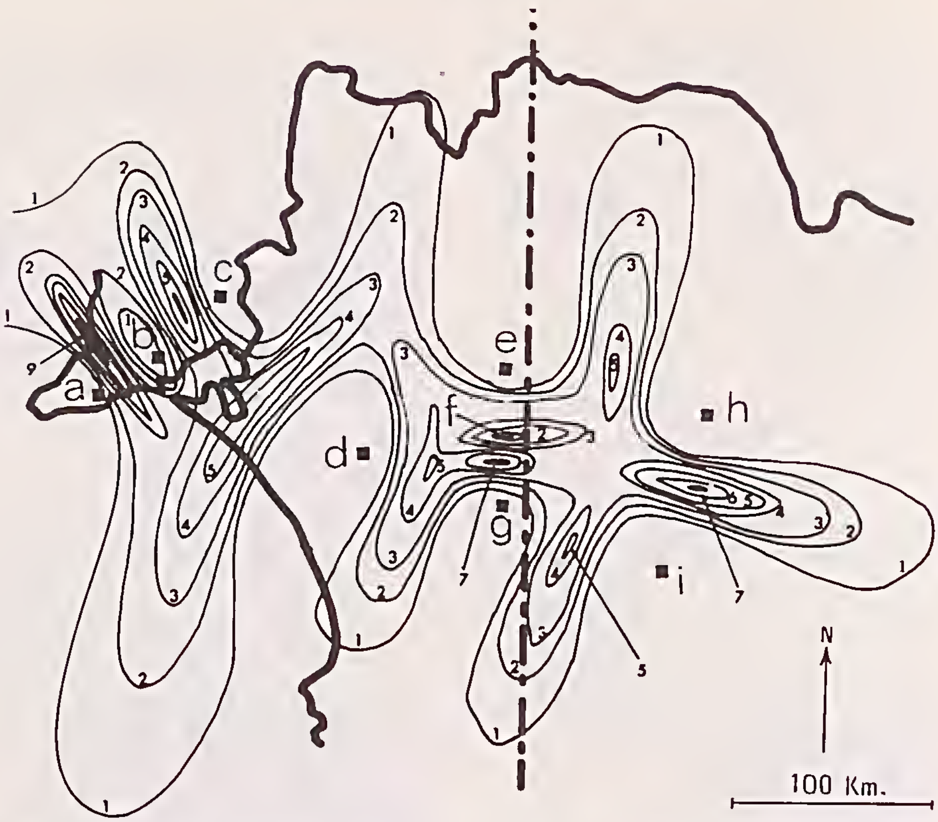

FIG. 6 — Contour plots for differential systematics of population means for all characters. The contour values are the average absolute differential of each of the characters. Population identities as for Fig. 5.
Contour values: 1 = 0.03, 2 = 0.05, 3 = 0.07, 4 = 0.09, 5 = 0.12, 6 = 0.14, 7 = 0.16, 8 = 0.18, 9 = 0.21

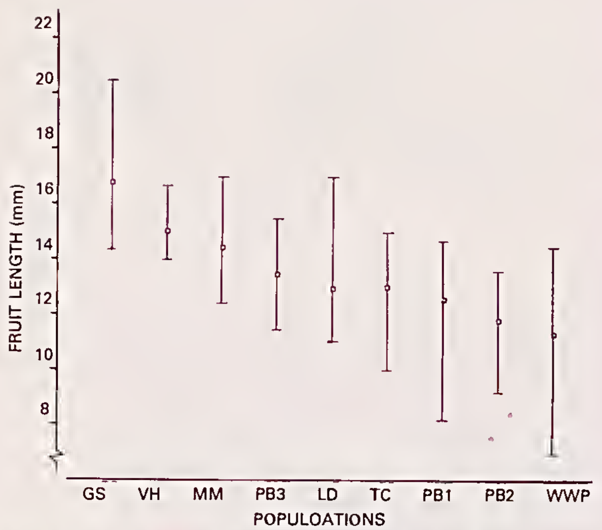

FIG. 7 — The mean (☐) and range (I) of the fruit lengths found in the populations.

exists. The characters which account for the total variation produce groups which indicate a progressive gradient across the study area.

DISCUSSION

Eucalyptus incrassata shows morphological variation without discontinuities across the study area. There is no evidence to suggest that the varieties *angulosa*, *costata* and *incrassata* are sufficiently distinct in terms of morphology and distribution to be regarded as separate species. The morphological changes observed can be explained as a cline extending from var. *angulosa* in the west to var. *incrassata* in the east. The clinal variation observed appears to be correlated to the amount of water available to the trees (Fig. 2 and Appendix). Pryor (1976) has stated that clines of continentality are found in eucalypts extending inland from the coast and that these are often correlated with increasing aridity. The inland forms of such a cline

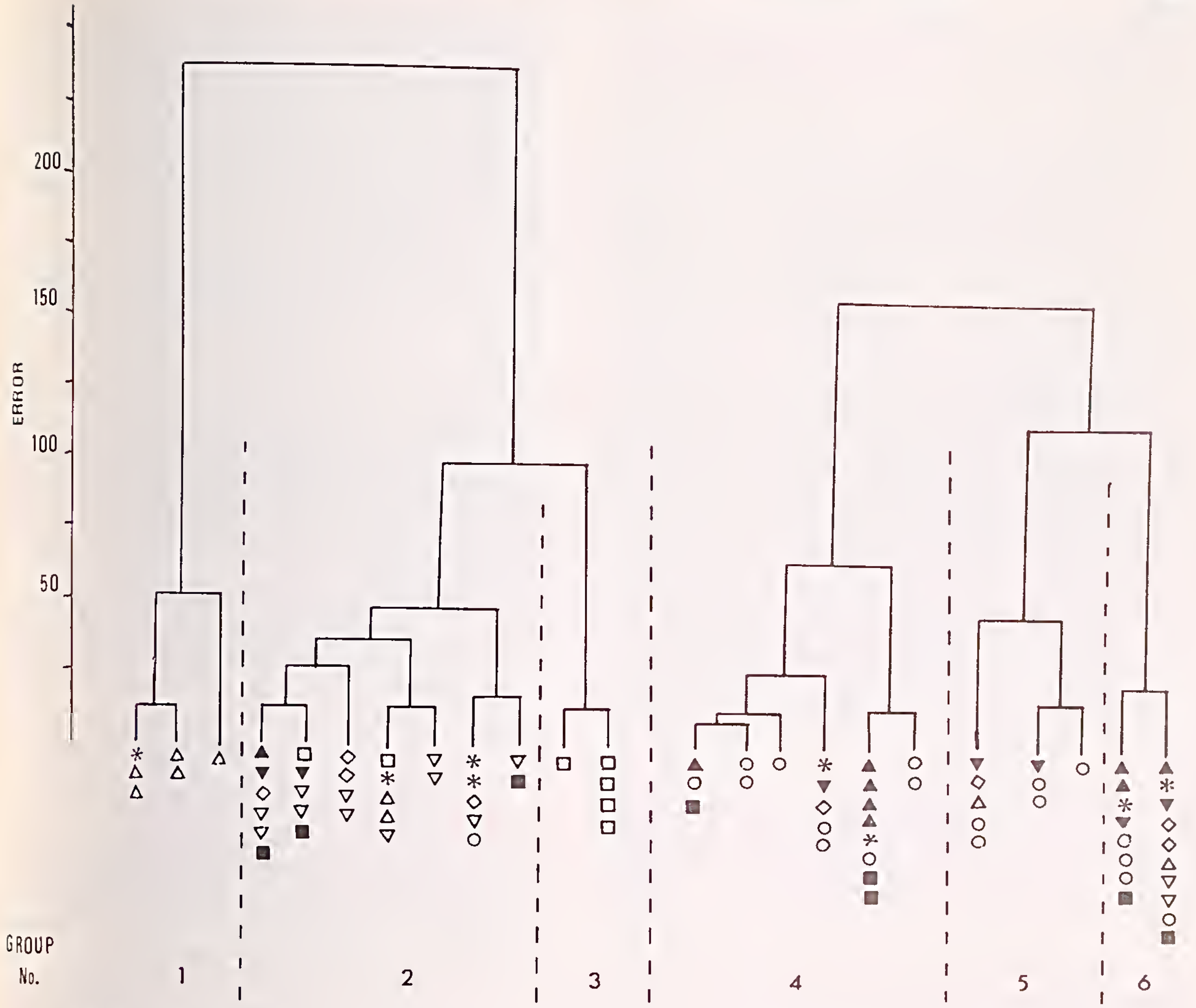

FIG. 8 — Hierarchical grouping of specimens collected using those characters which separate the populations.

Key to populations:
□ = VH, Δ = GS, ▽ = MM, ◇ = TC,
▲ = PB(1), ■ = PB(2), ▼ = PB(3)
O = WYP, * = LD

possess smaller organs (fruit and leaves) than the coastal forms. The cline of *E. incrassata* appears to be of this type.

Chippendale (1973) records var. *angulosa* in the very arid Nullarbor-Roe Plain region. This suggests that factors other than rainfall may be responsible for the variation of the species. The distributions given by Chippendale (1973) for var. *angulosa* and var. *incrassata* support the notion that a cline of continentality exists: the cline appears to be correlated to a sea/land gradient. Distance from the coast is the only common factor readily observable which explains the apparent variation pattern.

A continuous series of morphological forms was found in samples from nine arbitrarily selected sites in the 60,000 km^2 study area. The absence of discontinuities between the morphological extremes of *E. incrassata* (i.e. var. *incrassata* and var. *angulosa*) is good evidence for the incorporation of the taxa, var. *incrassata*, var. *costata* and var. *angulosa*, in one species. The correct name for this species is *E. incrassata* Labill. which has priority over *E. angulosa* Schauer and *E. costata* Behr. et Muell. cx Miquel.

Clinal variation presents problems with the nomenclature of the species involved. One of the prerequisites of a satisfactory classification scheme is its

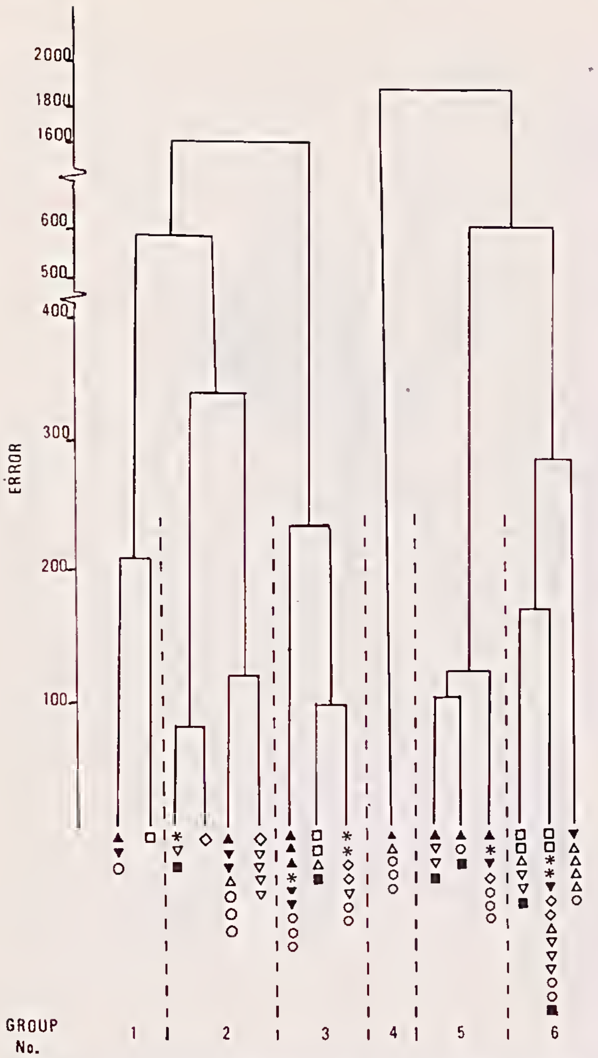

FIG. 9 — Hierarchical grouping of specimens collected using those characters correlated to factors.
Key to populations:
□ = VH, Δ = GS, ▽ = MM, ◇ = TC,
▲ = PB(1), ■ = PB(2), ▼ = PB(3)
O = WYP, * = LD

ability to permit accurate identification of the species of individual samples and to account for differences in morphology. Chippendale (1973, 1976) regards the taxon *E. angulosa* to be a valid species (Chippendale 1977 pers. comm.). The term species implies that the taxa are distinct entities (Davis & Heywood 1963). Pryor (1956) proposed that the term 'cline-form' be used to identify reference points within a cline, but this term has not been generally accepted (Pryor & Johnson 1971). The most satisfactory means of describing a cline in terms of nomenclature is to establish a series of infra-specific categories which provide reference points for the cline. Sub-species are major morphological subdivisions of the species, while the term variety implies a localized, morphologically distinct group within a species (Davis & Heywood 1963). The term 'sub-species' is preferable to 'variety' for naming 'cline-forms' as it implies that populations, rather than scattered individuals are being classified (Pryor & Johnson 1971).

The classifications of *E. incrassata* vary in the infra-specific epithets used. In explaining the cline observed, the most useful classification is that of Burbidge (1947) in which three varieties exist: *E. incrassata* Labill. *sensu stricto*, *E. incrassata* var. *costata* Burbidge, *E. incrassata* var. *angulosa* Benth. This classification is a reference to the end points, as well as to the centre of the range, and such a classification is necessary to describe clines (Jackson 1960). To clarify the meaning of *E. incrassata* Labill. *sensu stricto* Boomsma (1969) proposed the epithet *E. incrassata* var. *incrassata*.

The appropriate nomenclature for the *E. incrassata* group should be based on that of Burbidge but substituting the term sub-species for variety. The use of Boomsma's infra-specific epithet *incrassata* in place of *sensu stricto* provides a more suitable combination. The proposed nomenclature is as follows.

Eucalyptus incrassata Labill., 1804

(a) *Eucalyptus incrassata incrassata*

The type specimen for the species is located in the Florence Herbarium, Italy. Boomsma (1969) has examined photographs of the specimen. The type is apparently a good example of the taxon.

Distinctive features of taxon: mature fruit 7-12 mm long x 6-10 mm diam.; fruit surface smooth to striate. This taxon can be applied to the populations WYP, PB(1), PB(2), and TC.

(b) *Eucalyptus incrassata costata* (Behr. et Muell. ex Miquel) Johnstone et Hallam. Stat. nov.
Eucalyptus costata Behr. et Muell. ex Miquel, 1859

Distinctive features of taxon: mature fruit 11-17 mm long x 10-13 mm diam.; fruit surface costate. This taxon can be applied to the populations MM, LD and PB(3).

(c) *Eucalyptus incrassata angulosa* (Schauer) Johnstone et Hallam, Stat. nov.
Eucalyptus angulosa Schauer 1843

Distinctive features of taxon: mature fruit 14-23 mm long x 10-14 mm diam.; fruit surface costate to angular. This taxon can be applied to the populations VH and GS.

The purpose of proposing three infra-specific taxa is to facilitate accurate identification of *E. incras-*

sata specimens. Not all specimens will fit easily into a taxon. The continuous series of forms means that intermediates between the taxa will occur. Such cases can be determined with care or left as 'intermediate'

Previous authors (Chippendale 1973, Burbidge 1947) have distinguished the taxa mainly on the basis of ribbing of the fruit surface. The strong correlation between fruit size and surface ribbing gives a more readily quantifiable character for identification, such that the infra-specific taxa can be identified by using a combination of these characters.

CONCLUSION

E. incrassata shows a cline of continentality extending in an easterly direction inland from the coast in the region of the Murray River mouth. This cline encompasses the taxa *E. angulosa, E. costata* and *E. incrassata*. In view of this apparent clinal variation three infra-specific taxa have been proposed; these provide reference points within the cline as an aid to the identification of *E. incrassata* individuals.

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APPENDIX 1

LOCATION OF COLLECTION SITES

Population Code	Location	Rainfall* (cm/yr)
WYP	Wyperfeld National Park north-west Victoria [Ring Road, Brambruk Track & Dattuck Track (western 4 miles)].	33
LD	Little Desert National Park western Victoria (site nr. former Kiata Lowan Fowl Sanctuary).	38
TC	South side of Dukes Highway, 1 mile east of Culburra.	46
GS	Western side of the main Goolwa-Strathalbyn Road, 15 miles north of Goolwa.	48
VH	2 miles west of Victor Harbor, on coast road to Cape Jervis.	51
MM	Northern side of Dukes Highway, 1.5 miles west of Murray Bridge.	46
PB1	Eastern side of Pinnaroo-Bordertown Road, 11 miles south of Murray Bridge turn-off.	41
PB2	Parking Bay, eastern side of Pinnaroo-Bordertown Road, 32 miles south of Murray Bridge turn-off.	44
PB3	Pinnaroo-Bordertown Road, at turn-off to Keith, 15 miles north of Dukes Highway.	46

*Average annual rainfall recorded at nearest rainfall station. MM, PB1, PB2 and PB3 determined by interpolation.